

FOUR NEW WEST ATLANTIC SPECIES OF *TUBIFICOIDES* (OLIGOCHAETA, TUBIFICIDAE)

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Abstract.—Two species without hair setae are described from the Caribbean area: *Tubificoides panamensis*, from Panama and Bahamas, and *T. inops*, from Panama, Barbados and the Gulf of Mexico. The former is closely related to *T. motei* Brinkhurst, 1986 from Florida, but differs in setal numbers, shape of penis sheaths and morphology of spermathecal ducts. The latter lacks true penes and penis sheaths, but is included in *Tubificoides* as its genitalia in all other respects share apomorphies with those of all other species of that genus. *Tubificoides bruneli*, and *T. crinitus*, both with hair setae, are described from Lower St. Lawrence estuary (Québec, Canada) and the Gulf of Mexico, respectively. The first species has very stout spermatozeugmata, and ventral setae in anterior segments with upper teeth much longer than lower. *Tubificoides crinitus* is a small species occurring on the continental slope (down to at least about 550 m); its dorsal setae are all hair-like (alternating long and short within bundles). The generic definition of *Tubificoides* Lastockin, 1937 is emended, partly to accommodate the aberrant *T. inops*.

The marine tubificid genus *Tubificoides* Lastockin, 1937 has been subject to recent revision by Brinkhurst (1985, 1986), with subsequent additions to the list of species by Råsmark & Erséus (1986), Helgason & Erséus (1987), Milligan (1987), Erséus & Milligan (1989), Erséus (1989), and Erséus & Davis (1989). The present contribution describes four additional species of this large genus. Two of them possess, the other two lack hair setae in their dorsal bundles.

The material comes from (1) the author's own collection in Barbados (while at the Bellairs Research Institute of McGill University); (2) material from R.V. *Alpha Helix* cruise "CARIB. I." in 1977 (sorted by Smithsonian Oceanographic Sorting Center, SOSC, Washington, D.C.); (3) a collection from Andros Island, Bahamas [courtesy Dr. M. L. Jones, United States National Museum of Natural History (USNM), Washington, D.C.]; (4) samples from off Pascagoula, Mississippi, in the northern Gulf of Mexico (courtesy Mr. M. R. Milligan,

Mote Marine Laboratory, Sarasota, Florida); (5) oligochaetes from the St. Lawrence estuary, Québec (courtesy Prof. P. Brunel, Université de Montréal, Montréal, Québec, Canada); and (6) benthos from a study of the Northern Gulf of Mexico Continental Shelf (LGL Ecological Research Associates, Inc., Bryan, Texas, for Minerals Management Service).

Material collected by the author was fixed in Bouin's fluid, that collected by colleagues probably in formalin for most parts. Some specimens of *T. inops* were longitudinally sectioned and stained in Heidenhain's hematoxylin, all other worms were stained in paracarmine and mounted whole in Canada balsam. The type series are all deposited in the USNM.

Tubificoides panamensis, new species
Fig. 1

Holotype.—USNM 119870, whole-mounted specimen from N coast of

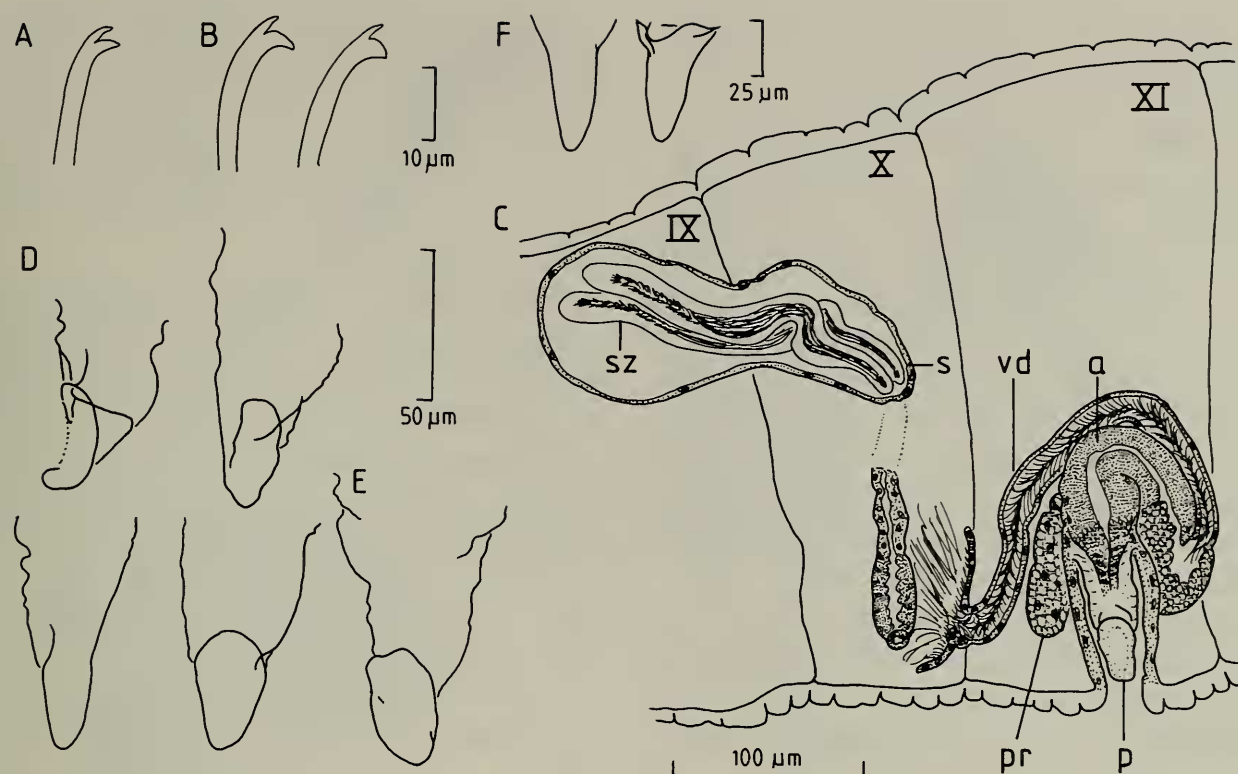


Fig. 1. A-E, *Tubificoides panamensis*: A, Anterior seta; B, Posterior setae; C, Lateral view of spermatheca and male genitalia in segments (IX)X-XI; D, Penis sheaths, specimens from Panama; E, Penis sheath, specimen from Bahamas; F, *Tubificoides motei* Brinkhurst: penis sheaths, specimens from Miami, Florida (coll. by author in 1977). Abbreviations: a, atrium; p, penis; pr, prostate gland; s, spermatheca; sz, spermatozeugma; vd, vas deferens.

Panama, Caribbean Sea, 90°34'36"N, 78°43'12"W, 0-4 m (30 Jun 1977); CARIB. I. *Alpha Helix* Stn. no. 23-333/149.

Paratypes. — USNM 119871-119873, three specimens from type locality. USNM 119874, one specimen from High Ridge Cay, Andros Island, Bahamas, 24°17'42"N, 77°45'12"W, subtidal, associated with *Thalassia* (5 Mar 1966); M. L. Jones Stn. no. 56.

Description. — Length 4.7-8.7 mm, up to 49 segments (some specimens not fully differentiated posteriorly). Width at XI 0.35-0.44 mm. Prostomium small, triangular. Postclitellar segments often elongate. Body wall naked anteriorly, with cover of particles tending to form papillae on small cuticular projections in postclitellar segments. Clitellum extending over XI-½XII. Setae all bifid, 45-65 μm long, two (rarely three) per bundle throughout most of body (generally reduced to one per "bundle" in cli-

tellar region and near posterior end), with upper tooth thinner and slightly shorter than lower; teeth more diverging in postclitellar (Fig. 1B) than in anterior setae (Fig. 1A), with lower tooth occasionally much longer than upper. Ventral, and generally also dorsal, setae absent from XI. Spermathecal pores in middle of X, between lateral lines and lines of ventral setae. Male pores in line with ventral setae in middle of XI.

Pharyngeal glands in IV-V. Esophagus somewhat enlarged in IX. Male genitalia (Fig. 1C) paired. Vas deferens 17-21 μm wide, thin-walled and ciliated, about 1.5 times longer than atrium, entering latter subapically opposite to entrance of prostate gland. Atrium small and curved, histologically tri- or bipartite (third, most ectal region not always distinct), about 165-175 μm long, entally 40-47 μm wide, at middle 23-33 μm wide, ectally 40-47 μm wide, with very thin outer lining of muscles. Ental part

of atrium heavily granulated; granulation similar to that of prostate gland. A short, granulated portion generally also discernible in ectal part of atrium, at base of penis. Prostate gland small, without discrete stalk. Penis (Figs. 1C, p; D–E) with cuticularized, conical penis sheath, with somewhat irregular, wrinkled outline and large oval lateral opening. Penis 65–95 μm long, basally 35–55 μm wide, at opening 16–28 μm wide. Spermathecae (Fig. 1C, s) with slender, 80–105 μm long, 23–20 μm wide ducts, and elongate ampullae; ectal half of ducts thickened and somewhat glandular, ampullae with slender spermatozeugmata.

Remarks.—*Tubificoides panamensis* appears closely related to *T. motei* Brinkhurst, 1986, known from Florida, but differs from that species by: (1) its lower number of setae (two, only rarely three, per bundle, as opposed to three, or even four, per bundle in anterior segments of *motei*); (2) its less smoothly funnel-shaped penis sheaths, which exhibit very distinct lateral openings [penis sheath openings not as distinct in specimens of *motei* from Miami in my possession (see Fig. 1F); it should be noted, however, that according to Brinkhurst (1986: 1274, fig. 3), the narrow distal end of the penis sheath of *motei* is “possibly with an oblique opening”]; and (3) the thickened ectal halves of the spermathecal ducts (ducts ectally provided with a very short, round and hollow swelling in my material of *motei*).

Distribution and habitat.—Caribbean side of Panama, Bahamas. Subtidal to about 4 m depth. In Panama, the species was found together with *T. inops*.

Tubificoides inops, new species

Fig. 2

Holotype.—USNM 119875, whole-mounted specimen from N coast of Panama, Caribbean Sea, 09°34'36"N, 78°43'12"W, 0–4 m (30 Jun 1977); CARIB I. *Alpha Helix* Stn. no. 23-333/149.

Paratypes.—USNM 119876–119880, five whole-mounted specimens from type locality. USNM 119881–119885, one sectioned and four whole-mounted specimens from “the hole,” at Holetown, St. James, Barbados, 5–9 m, muddy silt (28 Oct to 1 Nov 1979; C. Erséus).

Other material.—Author’s collection: two sectioned and seven whole-mounted specimens from Carlisle Bay, Barbados, 3.5–6.5 m, muddy silt and sand (24–25 Oct 1979; C. Erséus); and three sectioned and five whole-mounted specimens from Holetown (see paratypes). M. R. Milligan collection: two whole-mounted specimens (one of which sexually immature) from off Pasca-goula, Mississippi, northern Gulf of Mexico, 30°11'42"N, 88°37'18"W, 13 m, medium to fine sand with silt and clay (22 Apr 1987).

Etymology.—The name *inops* is Latin for “poor, lacking,” alluding to the species’ lack of penes.

Description.—Length 3.1–6.6 mm, 24–45 segments; width at XI 0.23–0.42 mm. Prostomium small, generally rounded and shorter than wide; posterior segments often elongate. Body wall naked anteriorly, in postclitellar segments with cover of fine particles, generally aggregated into discrete, pointed papillae. Clitellum extending over XI–½XII. Setae all bifid, 50–75 μm long, two to five per bundle anteriorly, one to three per bundle in postclitellar segments, with upper tooth thinner than lower; upper tooth somewhat longer than lower and lower tooth bearing indistinct subdental ligament in anterior setae (Fig. 2A), upper tooth shorter than lower in postclitellar setae (Fig. 2B). Ventral setae sometimes absent from XI. Spermathecal pores immediately anterior to ventral setae, in middle of X; male pores paired in line with ventral setae in middle of XI.

Pharyngeal glands in IV–V. Esophagus somewhat enlarged in IX. Male genitalia (Fig. 2D–E) paired; vas deferens 8–13 μm wide, thin-walled and ciliated, about 1.5

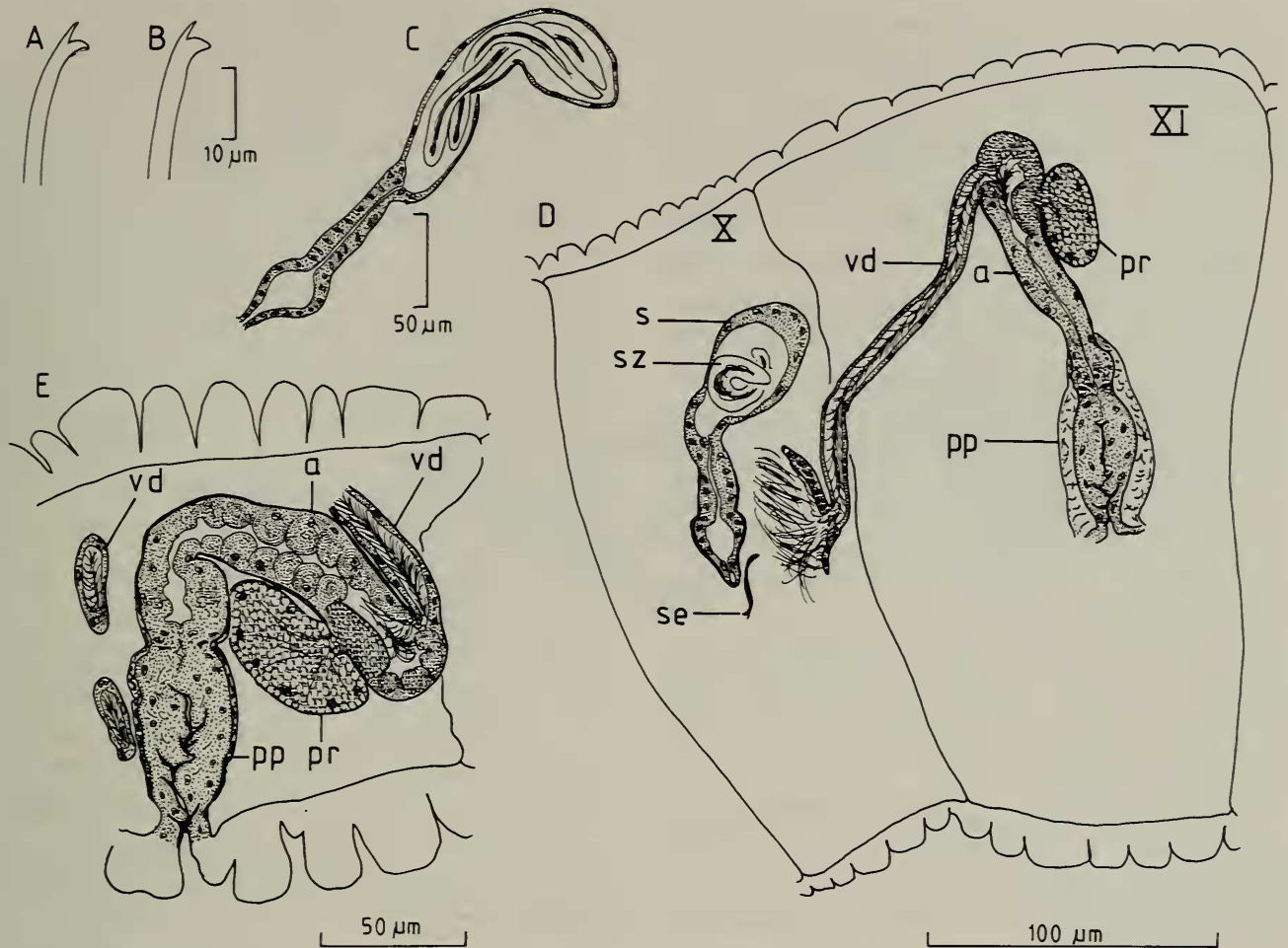


Fig. 2. *Tubificoides inops*: A, Anterior seta; B, Posterior seta; C, Spermatheca, specimen from Barbados; D, Lateral view of spermatheca and male genitalia in segments X–XI, whole-mounted specimen from Panama; E, Lateral section through male genitalia in segment XI, sectioned specimen from Barbados. pp, pseudopenis; se, seta; other abbreviations as in Fig. 1.

times longer than atrium, entering latter subapically opposite to entrance of prostate gland; atrium erect or curved, histologically tri- or bipartite (third, most ectal region not always distinct), 80–145 μm long, entally 23–40 μm wide, at middle 11–35 μm wide, ectally 21–39 μm wide, with about 1–2 μm thick outer lining of muscles; ental part of atrium granulated in a way different from that of other parts, sometimes some distinct granules also discernible in ectal part of atrium, at base of pseudopenis. Prostate gland compact, small, with smooth outline. True penis absent, instead copulatory sac, 35–65 μm long, 33–45 μm wide, modified into an (eversible?) pseudopenis; inner surface of sac lined with cuticle and folded in an irregular way. Spermathecae (Fig. 2C; D,

s) slender, with 55–115 μm long, 20–34 μm wide ducts, and thin-walled ampullae, ducts with roundish ectal swelling, ampullae containing slender spermatozeugmata.

Remarks.—The specimens from the type locality (Panama) have genitalia that are clearly smaller (Fig. 2D) than those of the worms from Barbados (Fig. 2C, E) and Gulf of Mexico.

The copulatory organs of *T. inops* are different from those of all congeners; they are pseudopenes rather than true, pendant penes. In fact, this feature disqualifies it for inclusion in the genus as currently defined (Brinkhurst & Baker 1979:1554): “. . . penial structure bearing a penis sheath of varying form.” However, its body wall papillation, characteristic atria and spermathecae

appear to be good synapomorphic characters shared with all "typical" members of *Tubificoides*. Then *T. inops* is either a very primitive member of the group (true penes had still not evolved when *inops*, or its ancestor, was split off from the rest of the lineage), or it is an advanced species within *Tubificoides* in the sense that its copulatory structure has "regressed" to an eversible pseudopenis. In the first case, *T. inops* could be hypothesized as the plesiomorphic sister group to the others and could be regarded as a monotypic genus, separate from *Tubificoides*. In the second case, it should (cladistically) be classified as a *Tubificoides*. Since most Tubificinae possess true penes, but do not possess the particular (advanced) atria found in *T. inops* (and in *Tubificoides* as a whole), the latter alternative seems the most parsimonious one.

Accordingly, the generic definition of *Tubificoides* is modified below to accommodate also *T. inops*.

Distribution and habitat. — Caribbean coast of Panama, Barbados, Gulf of Mexico. Subtidal silt and sand, to at least 13 m depth. In Panama, the species was found together with *T. panamensis*.

Tubificoides bruneli, new species

Fig. 3

Holotype. — USNM 119886, whole-mounted specimen from off Ile du Bic, Lower St. Lawrence estuary, Québec, Canada, 48°26'24"N, 69°00'00"W, 242 m, silt (31 Jul 1970; P. Brunel).

Paratypes. — USNM 119887–119890, four specimens from type locality.

Other material. — Author's collection: three specimens from type locality.

Etymology. — The species is named for Prof. P. Brunel (Département de Biologie, Université de Montréal), who provided the material.

Description. — Length more than 7.6 mm, more than 63 segments (no complete spec-

imens available); width at XI 0.37–0.50 mm. Prostomium variable in shape, rounded or triangular. Body wall with some scattered particles in postclitellar segments. Clitellum extending over XI–½XII. Dorsal bundles of II–VIII containing two to three bifid setae (Fig. 3A), up to 85 μ m long and with parallel, more or less equally long, slender teeth, and two hair setae, up to 200 μ m long; from IX, dorsal bundles containing one bifid or single-pointed seta (Fig. 3B), up to 85 μ m long, if bifid with teeth small and upper tooth longer than lower, and one hair, up to 145 μ m long. Ventral bundles of II–VIII with two to three bifid or single-pointed setae (Fig. 3C), up to 105 μ m long; if bifid, teeth slender and upper tooth much longer than lower; from IX, ventral setae single-pointed, up to 85 μ m long, one to two per bundle; ventral setae absent from XI. Spermathecal pores anterior to, and at some distance from, ventral setae, anterior to middle of X; male pores in line with ventral setae, posterior to middle of XI.

Pharyngeal glands in IV–V. Esophagus not particularly enlarged in IX. Male genitalia (Fig. 3E) paired; vas deferens 16–22 μ m wide, thin-walled and ciliated, several times longer than atrium, but exact length not established. Entrance of vas into atrium not observed, but probably subapical as in all congeners; atrium curved, histologically tripartite, 340–430 μ m long, entally 60–70 μ m wide, at middle 50–65 μ m wide, ectally 50–90 μ m wide, with thin outer lining of muscles; ental and ectal parts of atrium granulated in a way different from that of middle part. Prostate gland large, lobed. Penis (Fig. 3D; E, p) with cuticularized, smooth, funnel-shaped penis sheath with ectal ends characteristically distended and curved (opening terminal), 105–120 μ m long, basally 50–65 μ m wide, at distended ectal ends 28–42 μ m wide. Spermathecae (Fig. 3E, s) with 70–80 μ m long, 41–47 μ m wide ducts, and thin-walled, roundish ampullae; ducts with oval ectal swelling, lumen of which

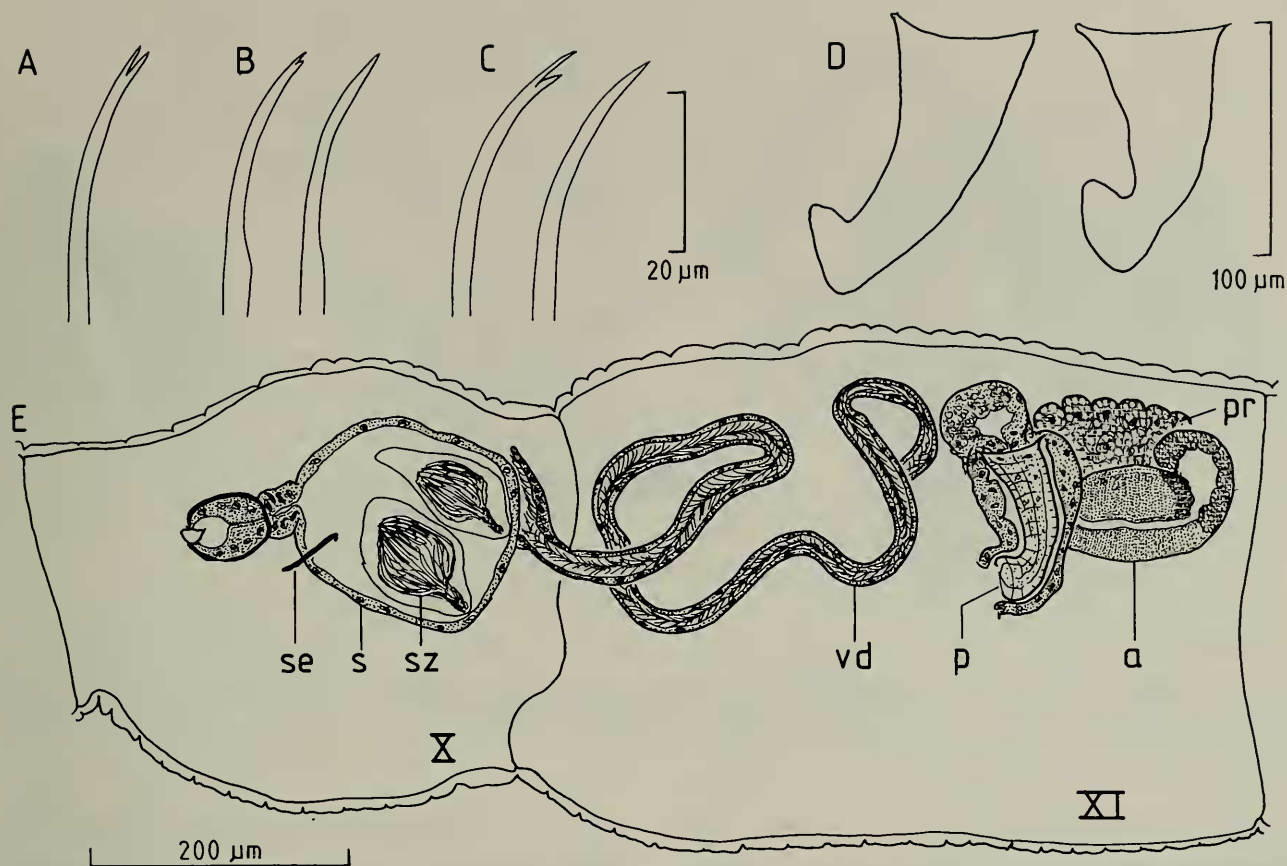


Fig. 3. *Tubificoides bruneli*: A, Dorsal anterior seta; B, Dorsal postclitellar setae; C, Ventral anterior setae; D, Penis sheaths; E, Lateral view of spermatheca and male genitalia in segments X–XI. Abbreviations as in Figs. 1–2.

hollow near pore, ampullae with very stout, or (in one paratype only) slender, spermatzeugmata (Fig. 3E, sz).

Remarks.—Only two additional species in the genus have single-pointed ventral setae in postclitellar segments, viz., *T. palacoleus* Baker, 1983 and *T. cuspietosus* Baker, 1983. The new species is, however, easily distinguished from both of these by its very characteristic penis sheaths; the penes are straight in the other two, those of *T. palacoleus* being provided with a strongly flared tip, those of *T. cuspietosus* being very slender. The shape of the penis sheaths (Fig. 3D), as well as the very long upper tooth of at least some of the anterior ventral setae (Fig. 3C), in fact distinguish *T. bruneli* from all congeners. The similarities in the outline of the penis sheaths with that found in *T. crenacoleus* Baker, 1983 is superficial; whereas the tip of the sheath is properly

curved in *T. bruneli*, it is more or less straight, but bears a lateral, blunt projection, in *T. crenacoleus*.

The very stout spermatzeugmata found in all but one of the postcopulatory specimens in the available material (spermatzeugmata of “normal,” slender type found in one worm only) are also noteworthy; spermatzeugmata with a similar shape have previously only been reported for *T. aculeatus* (Cook, 1970) (cf. Cook 1970: fig. 2D).

Distribution and habitat.—Known only from the type locality in the St. Lawrence estuary, Canada. Subtidal, silty sediment, 242 m depth.

Tubificoides crinitus, new species
Figs. 4–5

Holotype.—USNM 119891, whole-mounted specimen from S of Louisiana,

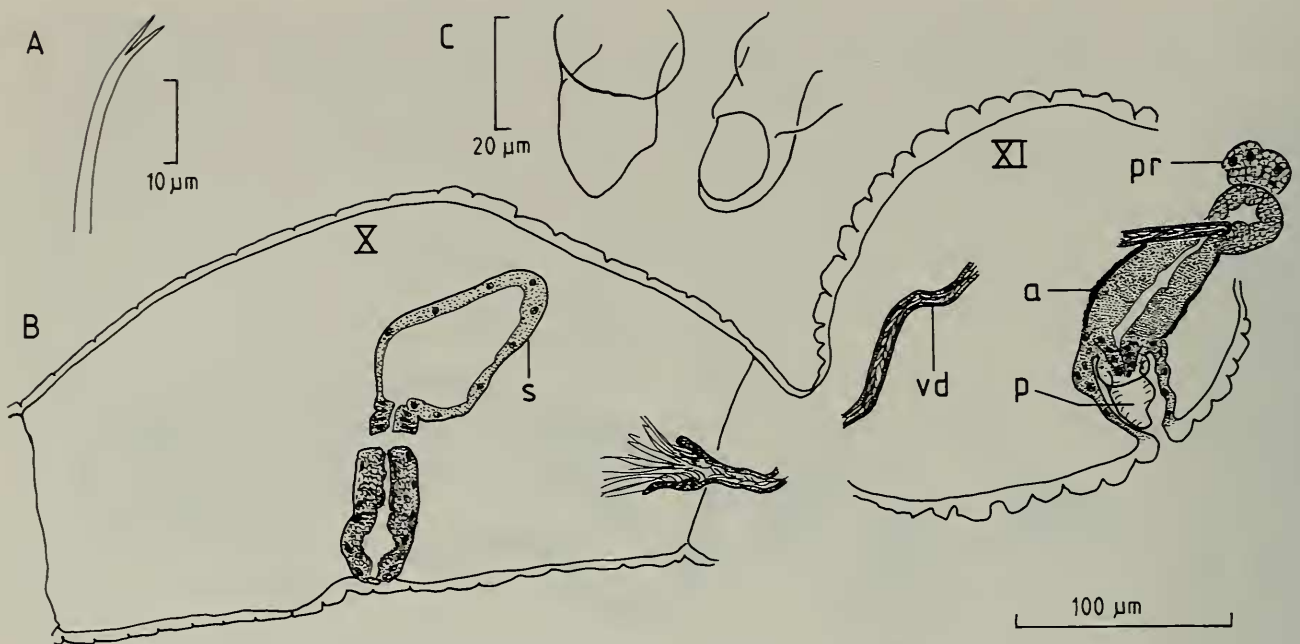


Fig. 4. *Tubificoides crinitus*, holotype: A, Ventral anterior seta; B, Lateral view of spermatheca and male genitalia in segments X–XI; C, Penis sheaths. Abbreviations as in Fig. 1.

27°43'07"N, 92°53'18"W, 349 m (Minerals Management Service, Northern Gulf of Mexico Continental Shelf Study; 7 Jun 1985).

Paratypes. — USNM 119892–119895, four specimens: one from type locality; one from 27°43'23"N, 92°53'23"W, 335 m (7 Jun 1985); one from 27°50'29"N, 90°44'06"W, 547 m (13 Jun 1985); and one (immature) from 28°34'42"N, 90°14'06"W, 320 m (26 Nov 1983).

Etymology. — The name *crinitus* is Latin for "having hair, hairy," referring to the species' possession of hair-like setae throughout the dorsal bundles.

Description. — Length and segment number unknown (specimens not complete), but worms appear very small. Width at XI 0.13–0.22 mm. Prostomium small, blunt, at least partially retractable. Body wall naked anteriorly, with some fine particles in postclitellar segments (but very few postclitellar segments remain on available worms). Clitellum poorly developed. Anterior dorsal bundles with one to three hair-like, single-pointed crotchets, 65–85 µm long, and one to three hair setae, 125–175 µm long; postclitellar dorsal bundles with two short hair-like setae, one slightly longer than the other;

ventral bundles with (one) two to three bifid setae (Fig. 4A), 60–80 µm long, with very slender, thin and almost parallel teeth; teeth equally long. Ventral setae of XI absent. Spermathecal pores in line with (and near) ventral setae in middle of X; male pores in line with ventral setae slightly posterior to middle of XI.

Pharyngeal glands in IV–V. Esophagus somewhat enlarged in IX. Male genitalia (Figs. 4B, 5) paired; vas deferens 8–11 µm wide, thin-walled and ciliated, at least about three times longer than atrium, entering latter subapically. Atrium of varying shape and length, histologically bi- or tripartite, 80–185 µm long, 30–42 µm wide, with up to 3 µm thick lining of (circular) muscles; ental part of atrium heavily granulated, remaining part less so. Prostate gland small, appears to be attached to atrium at some distance from apical end (see Fig. 5). Penis (Figs. 4B, p; C; 5, p) with cuticularized, cone-shaped penis sheath possessing large subterminal opening; penis 37–47 µm long, basally 23–26 µm wide, ectally 16–19 µm wide. Spermathecae (Fig. 4B, s) with 65–95 µm long, 28–36 µm wide ducts, and roundish to oval, small ampullae; ducts appear glandular, each with a roundish and hollow ectal

swelling; ampullae empty in holotype, with a few poorly preserved, slender, spermatozeugmata in one paratype.

Remarks.—Two other species of *Tubificoides* lack bifid setae throughout the dorsal bundles: *T. aguadillensis* Milligan, 1987, from Puerto Rico, and *T. uncinatus* Helgason & Erséus, 1987, from off the east coast of the U.S.A. These species, as well as *T. crinitus*, are also characterized by the somewhat aberrant location of the prostate gland on the atrium; the prostate is not attached to atrium opposite to entrance of vas deferens, but at a considerable distance from the apical end of the atrium (cf. Milligan 1987:fig. 4C; Helgason & Erséus 1987:fig. 6A). Both *T. aguadillensis* and *T. uncinatus* differ, however, from *T. crinitus* by having bifid (ventral) setae with short, i.e., “normal,” teeth, and the penis sheaths of *T. aguadillensis* are evenly conical with a small terminal opening (penis sheaths of *crinitus* not as evenly tapering and with a large subterminal opening), those of *T. uncinatus* are long and cylindrical and provided with a large subapical spur.

The spermathecae of the available material of *T. crinitus* are smaller and with stouter ducts and ampullae than those of most other species of the genus. However, as most of the studied specimens are precopulatory, this feature should be used with some caution; other, postcopulatory, worms of *T. crinitus* may have larger spermathecae than those described here.

A species very similar to *T. crinitus* is simultaneously described from a hydrocarbon seep area in the northern Gulf of Mexico by Erséus & Milligan (1989).

Distribution and habitat.—Known only from the northern Gulf of Mexico. Subtidal on outer part of continental shelf, 320–547 m depth.

Tubificoides Lastockin, 1937

Definition (emended).—A species-rich group of marine and brackish-water tubificids (subfamily Tubificinae). Body wall na-

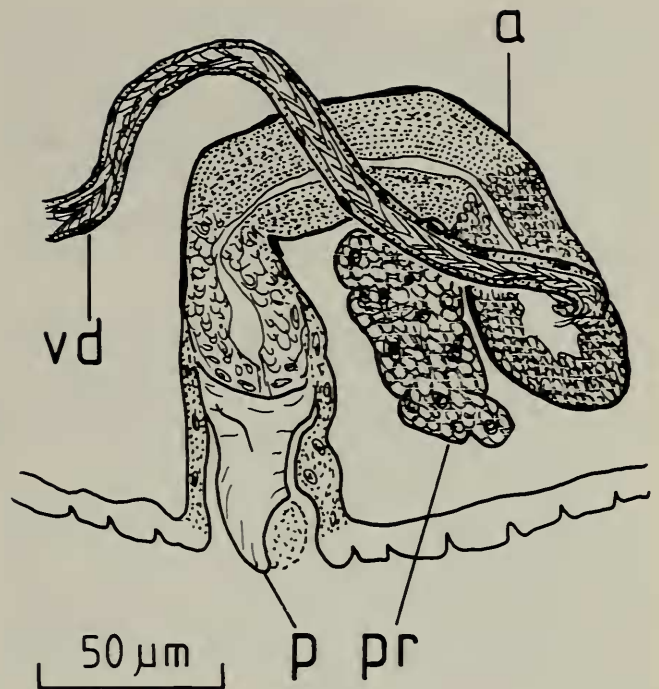


Fig. 5. *Tubificoides crinitus*, paratype: male genitalia. Abbreviations as in Fig. 1.

ked, or with fine particles adhering to cuticle, often forming distinct papillae. In most heavily papillated species, prostomium often retractable. Hair setae absent or present in dorsal bundles; when present, generally together with single-pointed, bifid or pectinate crotchets. Posterior dorsal setae, at least, frequently reduced to a single-pointed form barely distinguishable from the short hair setae where these are present. Modified genital setae absent. Male pores paired, more or less in line with ventral setae in posterior part of segment XI. Spermathecal pores paired more or less in middle of X.

Coelomocytes, if present, small and sparse, not of the “rhyacodriline-type.” Male efferent ducts paired in XI. Vas deferens ciliated, thin-walled, entering atrium subapically, generally opposite to large prostate gland. Rounded inner end of atrium cap-like, very heavily granulated and histologically different from rest of atrium. Main body of atrium cylindrical, generally curved; terminal part often again histologically distinct. Atrium terminating in a copulatory sac, which in all but one species contains a pendant penis bearing a cuticular penis sheath (in *T. inops* the copulatory organ is

modified into a complex, probably eversible, pseudopenis). Spermathecae consisting of a cylindrical duct, which often bears a distinct swelling near the ectal pore, and a round or oval-to-pear-shaped ampulla. Latter with spindle-shaped, often very slender, spermatozeugmata in postcopulatory specimens.

Type species. — *Tubificoides heterochaetus* Lastockin, 1937 = *T. swirencowi* Jaroschenko, 1948 [not *T. heterochaetus* (Michaelsen, 1926)] (see Brinkhurst & Baker 1979).

Remarks. — This definition is an extended and partly revised version of the latest one by Brinkhurst & Baker (1979:1554). The shape of the atrium (with the cap-like apical part and the subapical entrance of the vas deferens) should probably be regarded as the single most important synapomorphy for the genus. This is why *T. inops*, which lacks proper penes, is included (see further Remarks for *T. inops* above).

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